Galvezia leucantha subsp. *porphyrantha* (Scrophulariaceae), a New Shrub Snapdragon Endemic to Santiago Island, Galapagos, Ecuador

Alan Tye and Heinke Jäger

Department of Plant and Invertebrate Sciences, Charles Darwin Research Station, Isla Santa Cruz, Galapagos, Ecuador. Mailing address: CDRS, Casilla 17-01-3891, Quito, Ecuador. atye@fcdarwin.org.ec and heinke@fcdarwin.org.ec

ABSTRACT. We describe a distinctive subspecies of *Galvezia leucantha* from the island of Santiago (San Salvador), Galapagos, Ecuador. The new subspecies, *Galvezia leucantha* subsp. *porphyrantha* Tye & H. Jäger, is distinguished principally by its purple flowers and lack of pubescence. All three subspecies, and the species as a whole, have small and in some cases declining populations restricted to eroded scoria cliffs, and are considered Critically Endangered (CR) by IUCN criteria.

RESUMEN. Describimos una subespecie distintiva de *Galvezia leucantha* de la Isla Santiago (San Salvador), Galápagos, Ecuador. La nueva subespecie, *Galvezia leucantha* subsp. *porphyrantha* Tye & H. Jäger, se distingue principalmente por sus flores purpúreas y su falta de pubescencia. Las tres subespecies, y la especie en sí, tienen poblaciones pequeñas, en ciertos casos en declinación, restringidas a acantilados de escoria erosionados, y se consideran En Peligro Crítico de Extinción (CR) según los criterios de la UICN.

The genus *Galvezia* Dombey (Scrophulariaceae: Antirrhineae) comprises five species of the arid coastal zone of Peru, continental Ecuador, and the Galapagos Islands (Elisens, 1989, 1992). The single Galapagos species, the Galapagos Shrub Snapdragon, *G. leucantha* Wiggins (1968), is endemic to the islands, occurring in restricted cliff habitats. It has a distinct floral morphology and pollination biology when compared with its red-flowered, hummingbird-pollinated mainland relatives. Elisens (1989) drew attention to the paler flowers and shorter corolla tube of *G. leucantha.* Wiggins (1968) suggested that the white flower of the Galapagos species was pollinated by nocturnal moths or butterflies, although Elisens (1989) reported pollination by the endemic carpenter bee *Xylocopa darwini.*

Two subspecies of *G. leucantha* have so far been formally recognized: *Galvezia leucantha* subsp. *leucantha* of the western Galapagos islands Isabela and Fernandina, and *Galvezia leucantha* subsp. *pubescens* Wiggins (1968) on Rábida Island. *Galvezia leucantha* subsp. *leucantha* has white flowers and largely glabrous stems, leaves, pedicels, and calyces, while *Galvezia leucantha* subsp. *pubescens* was differentiated by the pink interior of the corolla and densely glandular-puberulent young twigs, leaves, pedicels, and calyces (Wiggins, 1968; see also Wiggins & Porter, 1971). *Galvezia leucantha* subsp. *pubescens* was also reported to have shorter pedicels, and to be dimorphic in flower color (Elisens, 1989), confirming the statement in Wiggins and Porter (1971) that the interior of the corolla is "sometimes" reddish or pink.

In addition to the two named subspecies, Elisens (1989) recognized a third, unnamed form from Santiago (San Salvador) Island. Two populations from Santiago, on old red hills in recent black lava flows, were studied by Elisens (1989): one at James Bay (west coast) and the other behind Bahía Ladilla (southwest coast). Elisens compared several characters between the populations on Santiago (two), Rábida, Isabela (two), and Fernandina. He also examined isozyme variation at 26 loci, of which 24 were invariant among all six populations, and the other two had only two alleles each, with variation present in only one population (Rábida and James Bay) for each of these two loci. Further, the two populations with polymorphic loci contained few heterozygotes. This lack of genetic variability has been found in other Galapagos endemic plants (Rick & Fobes, 1975; D. Anderson, pers. comm. 1999), as in other radiative groups on oceanic islands (e.g., Lowrey & Crawford, 1985; Crawford et al., 1987; T. Lowrey, pers. comm. 1999).

Compared with the lack of intrapopulation variation in genetic and morphological characters, interpopulation morphological variation is marked and consistent (Elisens, 1989), which probably reflects founder effects and genetic drift in the very small populations (mostly fewer than 50 plants).

Recent fieldwork on Santiago Island has enabled the re-examination of the populations previously studied by Elisens (1989), as well as another population in the east-central part of the island. The new material confirms the distinctiveness of the Santiago populations, which we name:

Galvezia leucantha subsp. **porphyrantha** Tye & H. Jäger, subsp. nov. TYPE: Ecuador. Galapagos, Santiago Island: red hill in Bahía Ladilla, 0°18′5″S, 90°49′40″W, 13 Nov. 1998, *H. Jäger & A. Tye, CDRS 9338* (holotype, CAS; isotypes, CAS, CDS).

Haec subspecies a subsp. *leucantha* corolla extus magentea, intus striis roseis albisque ornata atque corollae labii superioris lobulis apice albis differt.

Shrub, much branched at base, with branches suberect, horizontal to (on cliffs) pendent, to 1.5 m long. Leaves opposite, blades up to 5 × 5.2 cm, elliptic-lanceolate to ovate-lanceolate, broadly cuneate to rounded at base, acute at apex, entire, bright green, glabrous, occasionally sparsely puberulent; petioles 5–7 mm long. Flowers axillary. Pedicels slender, 10–17 mm but lengthening to 25 mm in fruit, glabrous, spreading-ascending, bent abruptly at apex; calyx with cup of fused basal part of sepals delineated from sepal lobes by groove, lobes acute to obtuse, 1.5–2.5 mm long, glabrous, but slightly puberulent along margins; corolla 6.5–12.5 mm long, outside puberulent, reddish purple, inside irregularly striated pink and white, tips of superior petal lobes white, corolla tube 4.5–6.5 × 1.5 mm, slightly ampliate, the limb bilabiate, superior lip 2–5.5 mm, bilobed about halfway to base, lobes cucullate to spreading-ascending, puberulent, lower lip trilobate, 1.5–4 mm long, base of lower lip folded, glandular-puberulent, sinuses between lobes ca. 2 mm deep, central lobe cucullate; posterior pair of stamens ca. 5 mm long, filaments glabrous; anterior stamen pair longer, ca. 7 mm, filaments glabrous distally, glandular-papillate basally; anthers ca. 1 mm long; fifth stamen sterile, inserted ca. 1.5 mm above base of tube, ca. 2 mm long; capsules subglobose, 3–5 mm long; seeds 0.5–0.7 mm long, subtruncate, with 4 to 7 cristate-echinate longitudinal ridges, black. A photograph of the flower of the new subspecies appears in Elisens (1989: fig. 1).

We assign this form the rank of subspecies, since it is a morphologically recognizable and well-defined form, and occurs in a geographical area allopatric with the other forms.

Etymology. We choose the name *porphyrantha* to correspond with the descriptive names of the other taxa, and based on the most obvious difference from them. The full name of the subspecies is thus the purple-flowered, white-flowered *Galvezia.*

Discussion

Holotype. This specimen bears the original specimen number *CDRS 9338B* assigned by the Herbarium of the Charles Darwin Research Station (CDS), before being deposited at the California Academy of Sciences (CAS). It is a fertile specimen bearing flowers and fruit, but it does not show the full range of variation in leaf size, with most leaves being small.

Isotypes. 1. Original CDS number *CDRS 9338C,* deposited at CAS. This specimen is from the same plant as the holotype, and is a branch with copious foliage but no flowers. Collection details are as for the holotype. 2. *CDRS 9338A,* deposited at CDS. This is a fertile branch bearing fruit, from the same plant as the holotype. Collection details are as for the holotype.

Paratypes. All paratype specimens are deposited at CDS. ECUADOR. **Galapagos, Santiago Island:** Bahía Ladilla, 28 June 1999, *A. Tye CDRS 9464*; James Bay, 11 Nov. 1998, *H. Jäger & A. Tye CDRS 9337A, 9337B*; James Bay, 2 Oct. 1995, *A. Mauchamp CDRS 6840*; crater in Zona D, 25 Feb. 1996, *I. Aldaz CDRS 6896A, 6896B.*

Characteristics of the three subspecies are compared in Table 1. The foliage, young twigs, pedicels, and calyces of all populations of *Galvezia leucantha* subsp. *porphyrantha* are glabrous or only sparsely pubescent, as in *Galvezia leucantha* subsp. *leucantha,* and unlike *Galvezia leucantha* subsp. *pubescens.* The flowers in all Santiago populations of the new subspecies are externally magenta, with white seen only on the superior lobes, and internally striated pink and white, as seen in the photograph presented by Elisens (1989: fig. 1).

Some other apparent differences between subspecies have been suggested, based on the few collections then available, which do not appear to be supported by the current larger collections including the new material. Leaf size does not reliably permit discrimination between subspecies: although the leaves of *Galvezia leucantha* subsp. *porphyrantha* are larger in some specimens than the largest mentioned by Wiggins and Porter (1971) for *Galvezia leucantha* subsp. *leucantha,* leaves as large as this were found in material from Isabela (Wiggins, 1968). Pedicels of all subspecies appear quite variable in length (Table 1), obscuring the differences that were suggested by Elisens (1989)

Table 1. Characteristics of three subspecies of *Galvezia leucantha*. Data are from Wiggins (1968) (W), Wiggins & Porter (1971) (WP: only for characters that differ from W), Elisens (1989) (E), and the current study (T). For flower measurements listed under "T" (made by AT), sample sizes are: *G. leucantha* subsp. *leucantha* n = 6 (4 from Isabela, 2 from Fernandina); *G. leucantha* subsp. *porphyrantha* n = 4; *G. leucantha* subsp. *pubescens* n = 4.

	subsp. *leucantha*, Isabela and Fernandina	subsp. *porphyrantha*, Santiago	subsp. *pubescens*, Rábida
Pubescence	None to sparse (W, E, T)	None to sparse (E, T)	Dense, glandular (W, E, T)
Corolla	White (W, E, T)	White, with violet on "upper two fused petals" (p. 102) or "tube" (p. 103, photo p. 99) (E) Externally magenta (all petals), with tips of superior lobes white (T)	White, inside sometimes reddish or pink (WP). Dimorphic: most white, very rarely violet-tinged (E, T)
Pedicel length (mm, in flower)	8–12 (W) 13–24 (E) 14–23 (Isabela) (T) 8–14 (Fernandina) (T)	12.5–14 (E) 10–17 (T)	10–12.5 (E) 10–17 (T)
Sepal length (mm)	4–6 (W) 2–3 (T)	1.5–2.5 (T)	2–2.5 (T)
Corolla length (mm)	10–12 (WP*) 7.5–9 (T)	6.5–12.5 (T)	8–9 (T)
Corolla tube length (mm)	5.5–6.5 (E) 8–10 (W) 4.5–5 (T)	5.5.–6.5 (E) 4.5–6.5 (T)	5–5.5 (E) 4–5 (T)
Superior corolla lip length (mm)	5–6 (W) 3–3.5 (WP*) 2–4 (T)	2–5.5 (T)	3–4 (T)
Inferior corolla lip length (mm)	2 (W) 3.5–4 (WP*) 1.5–2.5 (T)	1.5–4 (T)	2.5–3 (T)

* Characters given by WP for *G. leucantha* subsp. *leucantha* may include specimens of subspecies *porphyrantha*. In addition to the Santiago material quoted above, data for the other subspecies under "T" in this table are from specimens in CDS.

to exist between populations. The sepals of *Galvezia leucantha* subsp. *leucantha* appear to be shorter than recorded by Wiggins (1968) and Wiggins and Porter (1971). They are not as different from the presumed ancestral *G. fruticosa* Gmelin as suggested by Wiggins (1968), and there is no significant difference between Galapagos populations. The major point arising from the flower measurements in Table 1 is that, despite earlier suggestions of differences, the populations from all islands seem more or less similar with respect to the size of both leaves and flowers. All flower measurements are based on small samples, and the differences between subspecies and populations are not statistically significant. The corolla of the Santiago subspecies, when fully open, may average longer than that of most other populations, but further data would be required to confirm this. If so, then the new subspecies would most closely resemble mainland *Galvezia*, with their long, tubular, red corollas, in both flower color and form.

KEY TO THE THREE SUBSPECIES OF *GALVEZIA LEUCANTHA*

1a. Dense, glandular pubescence on young branches, pedicels, and calyces . . . . . *G. leucantha* subsp. *pubescens* (Rábida Island)

1b. Pubescence none or sparse.

2a. Flowers white . . . . . *G. leucantha* subsp. *leucantha* (Isabela, Fernandina)

2b. Flowers reddish purple . . . . . *G. leucantha* subsp. *porphyrantha* (Santiago)

EVOLUTION

Most *Galvezia* have long, tubular, red flowers adapted for hummingbird pollination (Elisens & Freeman, 1988). Elisens (1989) suggested that, despite the greater age of Rábida island, the Santiago populations, being morphologically closest to mainland relatives, may be older, with the whiter-flowered populations on the western Galapagos islands and Rábida being derived. The color of the flowers of the three subspecies of *G. leucantha* suggests an evolutionary and geographic progression from a sin-

gle colonization event, which perhaps initially established a now-extinct population on an eastern island (in support of Elisens, 1992). Divergence may have occurred from the original founder population, in two different directions on Santiago and Rábida, since the pubescence of the Rábida population is more similar to the state in mainland *G. fruticosa*, whereas the Santiago subspecies is most similar to mainland species in flower color and possibly floral structure. Both of these subspecies thus retain primitive but different characteristics. Populations furthest from the mainland (on the youngest islands) have diverged the most from the pubescent, red-flowered, mainland taxa, having both glabrous foliage and the palest, white flowers.

Galvezia leucantha has floral nectar characteristic of hummingbird-pollinated flowers, according to Elisens and Freeman (1988). This may not indicate a particularly recent origin for the species. Most other bee-pollinated relatives of *Galvezia* also have nectar characteristic of hummingbird-pollinated flowers (Elisens & Freeman, 1988) rather implying that nectar sugar composition is relatively invariant in the South American Antirrhininae. Elisens (1989) further showed that *G. leucantha* was self-compatible, although cross-pollination within and between populations gave higher levels of seed set. Although self-compatibility is common in island floras, it is, in the case of *Galvezia*, probably a primitive condition of the genus, as its mainland relatives are also self-compatible (Elisens, 1989).

Conservation

Given its restricted habitat, which comprises eroding, scoria cliffs that are the weathered remnants of comparatively old formations, and its presence on only four islands, the species is and always will be naturally rare. However, since the discovery of Galapagos almost 500 years ago, the plant has come under threat from introduced species, primarily large mammalian herbivores. Fernandina and Rábida islands are currently free of such animals. Fernandina has never had them, and the few goats that were present on Rábida in the 1970s were finally eradicated in 1977. Even though *Galvezia leucantha* has probably always been restricted to scoria cliffs, it may have been more common and widely distributed on Santiago and Isabela in the past. Both of these islands now have large populations of goats and donkeys, and *Galvezia* is now found virtually exclusively on those parts of the cliffs that are out of the reach of such animals. On these islands it is absent from gentler scoria slopes similar to those on which it occurs on Rábida. The species is also at risk from volcanic eruption, and it is likely that suitable habitat, at least on Santiago and possibly also on Fernandina and Isabela, may have been reduced by new lava flows in the last 200 years.

The Santiago populations are all small. In April 1999 there were about 50 plants at Bahía Ladilla and one plant at the unnamed crater in "Zona D." The site at James Bay consists of two old red cinder hills surrounded by a more recent black lava flow. In December 1999, the James Bay population comprised about 80 plants (including seedlings): the larger hill supported about 70, with the remaining 10 on the smaller. The larger hill is also the site of two plants of the Critically Endangered Santiago endemic *Scalesia atractyloides* Arnott var. *atractyloides* (Asteraceae), for which this appears to be the only remaining site. Following the discovery of these two plants, most of the hill, including the cliffs on which the *Galvezia* and *Scalesia* taxa are found, was surrounded by a goat-proof fence, in December 1998. This may permit expansion of the *Galvezia* population and should at least reduce its risk of disappearance. The site at Bahía Ladilla is similar, and formerly carried a small population of *Scalesia atractyloides*. The latter is now extinct there, although plants from that population are in cultivation at the Copenhagen Botanical Garden (O. Hamann & H. Adsersen, pers. comm. 1999). The *Galvezia* population is at present unprotected except by its ability to grow on vertical cliffs out of the reach of goats. The third population, at Zona D, is in a small crater, of old red scoria layered with basalt, where the only two known remaining plants of the other variety of *Scalesia atractyloides*, var. *darwinii* (Hooker f.) Eliasson, are also found. This site was fenced in 1997, which may enable the populations of these two species there to increase.

The critically small size of all populations of *G. leucantha*, and the recent reduction of the populations on Isabela and Santiago (Elisens, 1989, pers. obs.), result in the species as a whole meriting the IUCN (1994) classification Critically Endangered (= CR), by criterion C2a. *Galvezia leucantha* subsp. *pubescens* of Rábida is under no current grazing threat but qualifies as CR (D) by virtue of its tiny population (ca. 36 plants in December 1999, A. Tye pers. obs.), *Galvezia leucantha* subsp. *leucantha* qualifies as CR (B1, B2c, B2e) as it is under severe threat from goats and donkeys on Isabela, while *Galvezia leucantha* subsp. *porphyrantha* qualifies as CR (B1, B2c, B2e, C2a) given its recent declines.

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